IBIS
international journal of avian science
Ibis (2025) doi: 10.1111/ibi.13437

Short Communication

Sexual and social functions of ornamental wing feathers in Black Swans (*Cygnus atratus*)

ANDREW C. KATSIS[1,2,3] MARK A. ELGAR[1] &
RAOUL A. MULDER*[1]
[1] *School of BioSciences, University of Melbourne, Melbourne, Victoria, Australia*
[2] *Konrad Lorenz Research Centre for Behaviour and Cognition, University of Vienna, Grünau im Almtal, Austria*
[3] *Department of Behavioral and Cognitive Biology, University of Vienna, Vienna, Austria*

Studies on the evolution of ornamentation have traditionally focused on sexual selection, although ornaments may also signal an individual's quality in non-sexual contexts. Using wild-captured Black Swans *Cygnus atratus*, we conducted two-way association trials to study how a putative mutual ornament (curled wing feathers) influenced swans' intersexual and intrasexual preferences. When allowed to freely associate with two candidate birds matched for size and condition, focal males preferentially associated with the candidate with the higher number of curled wing feathers whereas focal females showed no consistent preference. Males preferred the more ornamented bird during both sexual trials (where both candidates were female) and social trials (where both candidates were male), supporting the hypothesis that monomorphic ornaments can function in both sexual and social interactions.

Keywords: *Cygnus atratus*, mate choice, mutual sexual selection, ornamentation.

Empirical studies of sexual selection have focused predominantly on organisms with sexually dimorphic traits, in which trait elaboration is typically restricted to males (Amundsen 2000), and there is abundant evidence that female choice and male–male competition can lead to the evolution of extravagant ornamentation in males (Jennions & Petrie 1997). However, females in many species also exhibit elaborate secondary sexual characters (Clutton-Brock 2009, Tobias *et al.* 2012). Indeed, it is increasingly clear that male choice and female–female competition, rather than being exceptions to the rule, are relatively common phenomena, especially in species where females compete intensely for breeding opportunities (Edward & Chapman 2011, Rosvall 2011, Hare & Simmons 2019). In these circumstances, sexual selection can produce traits that are more elaborate in females than in males (e.g. wing spurs in Wattled Jacana *Jacana jacana*; Emlen & Wrege 2004) or expressed to a similar degree in both sexes (e.g. ornamental crests in Crested Auklets *Aethia cristatella*; Jones & Hunter 1993).

This last category is perhaps the least understood. In their landmark study of Crested Auklets, Jones and Hunter (1993) found that both males and females performed more frequent sexual displays towards opposite-sex taxidermic models whose crests had been experimentally lengthened. These findings demonstrated that monomorphic ornamental traits could be favoured by mutual mating preferences. However, only a handful of empirical studies have explored this question further (e.g. in Bluethroats *Luscinia svecica*, Amundsen *et al.* 1997; and in Blue-footed Boobies *Sula nebouxii*, Torres & Velando 2005) and these studies generally limited their scope to the ornaments' inter-sexual functions. This focus is surprising, given that plumage characteristics can signal not only sexual attributes but also social dominance (Lyon & Montgomerie 2012, Clutton-Brock & Huchard 2013).

Black Swans *Cygnus atratus* are large Australian waterbirds in which both males and females possess prominent curled wing feathers (Kraaijeveld *et al.* 2004). The number of curled feathers remains relatively unchanged once an individual reaches maturity and shows more variation between individuals than other morphological traits (Kraaijeveld *et al.* 2004), a pattern typical of ornamental traits in birds (Cuervo & Møller 2001). Observational studies suggest that curled feathers probably play a role in mate choice: first, the feathers are highly visible during triumph ceremonies between breeding partners (Kraaijeveld & Mulder 2002) and, secondly, paired birds have, on average, a higher number of curled wing feathers than unpaired birds (Kraaijeveld *et al.* 2004). In addition, the number of curled feathers is highly correlated between mating partners, suggesting assortative mating with respect to this trait (Kraaijeveld *et al.* 2004). We know relatively little about the process of pair formation in Black Swans, so these pairing patterns could result from (1) phenotype-matching, where individuals seek out partners with ornament elaboration similar to their own, or (2) a mating market, where individuals prefer partners with the most elaborate ornaments but as a result of competition eventually settle for partners similar in ornamentation to

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*Corresponding author.
Email: r.mulder@unimelb.edu.au

themselves (Baldauf *et al.* 2009). In addition to sexual signalling, curled wing feathers may also function in Black Swan social dominance. The feathers are prominently visible during agonistic interactions and swans with more curled feathers were more likely to win these encounters (Kraaijeveld *et al.* 2004).

We designed a series of captive association trials to better understand the function of ornamental feathers in Black Swans. First, we established a captive colony of swans using wild-caught individuals from three source locations in Victoria, Australia. We then conducted association trials to test whether natural variation in the subjects' feather ornamentation predicted patterns of association between opposite-sex and same-sex individuals. Because feather ornamentation is sexually monomorphic in this species, we predicted that both male and female focal swans would show a preference for more ornamented birds.

METHODS

Study species

Black Swans are large (4–9 kg), long-lived waterfowl that commonly occupy permanent and temporary shallow wetlands (Frith 1982). The sexes are identical in appearance, although males are slightly larger. The species is socially monogamous and both sexes participate in incubation and brood defence. They have a low divorce rate, with pairs generally remaining together once formed (Kraaijeveld 2003). Both sexes display ornamentation in the form of curled feathers on their wings, which can range in number from 7 to 22 per wing (Kraaijeveld *et al.* 2004). The Black Swan is the only member of its genus to exhibit feather ornamentation, although other swan species, such as the Black-necked Swan *Cygnus melancoryphus* and Mute Swan *Cygnus olor*, possess elaborate bill ornaments instead (Kraaijeveld *et al.* 2004).

Source and housing of swans

In October 2008, we established a captive colony of 40 Black Swans at Serendip Sanctuary in Lara, Victoria, Australia (38°00′15″S, 144°24′39″E), using wild-caught individuals from three source locations elsewhere in Victoria: The Strand and Sandy Point, Williamstown (37°51′31″S, 144°54′08″E); Albert Park Lake, Melbourne (37°50′48″S, 144°58′17″E); and Lake Wendouree, Ballarat (37°33′03″S, 143°49′52″E). To minimize the likelihood of familiarity between males and females, we collected only males from Williamstown and only females from Albert Park Lake and Lake Wendouree. We estimated sex by cloacal examination and morphometric measurements and took a small blood sample from each bird to allow sex verification by polymerase chain reaction (Griffiths *et al.* 1998). All subjects were sexually mature adults at least 3 years old (pure white primary and secondary wing feathers; Braithwaite 1981) and most were known to be unpaired.

Each bird was fitted with a numbered stainless-steel band issued by the Australian Bird and Bat Banding Scheme and a coloured plastic neck collar engraved with a unique alphanumeric identification code. Captured individuals were then transported in animal carriers to Serendip Sanctuary. On arrival, two experimenters independently counted the number of curled wing feathers on each subject, using the procedure described in Kraaijeveld *et al.* (2004). Independent counts were highly correlated ($r_{(40)} = 0.86$, $P < 0.0001$) and differed by zero to four feathers, with no consistent observer biases (observers agreed six times, the first observer counted higher 19 times, and the second observer counted higher 16 times). We used the mean value between the two observers as the bird's final count of curled wing feathers. Using this measure, the mean ± standard error (se) number of curled wing feathers per bird was 22.6 ± 0.6 se (range 12–31.5). To prevent birds from escaping the enclosures, their primary wing feathers and first five secondary wing feathers were clipped near the base using scissors. This manipulation had no effect on the curled feathers, which are tertials and wing coverts. Clipped feathers are regrown annually at the time of moult. Experimental animals were returned to the wild after this moult had taken place, so that they had recovered flight capability.

Males and females were sexually segregated into two large (1 ha) enclosures containing 300-m^2 ponds at their southern end. The enclosures were separated by a dense brush fence, which prevented visual interactions between birds in adjacent enclosures. Each enclosure contained three feeding stations providing the swans with a daily *ad libitum* mixture of poultry grower's crumble and wheat, and lettuce leaves every second day, supplemented with fresh lawn clippings when available. Birds were kept in captivity for the duration of the experiment (about 6 weeks) from October to December 2008, which falls within the normal range of breeding dates for this species (Braithwaite 1981, Kraaijeveld *et al.* 2007b).

Association trials

In a series of association trials, we presented a 'focal' bird with two 'candidate' birds that were both either the same sex (social trial) or the opposite sex (sexual trial) as the focal individual. Association trails were conducted in a large octagonal enclosure (Fig. 1), comprising a central chamber (7.0 m in diameter, with a large

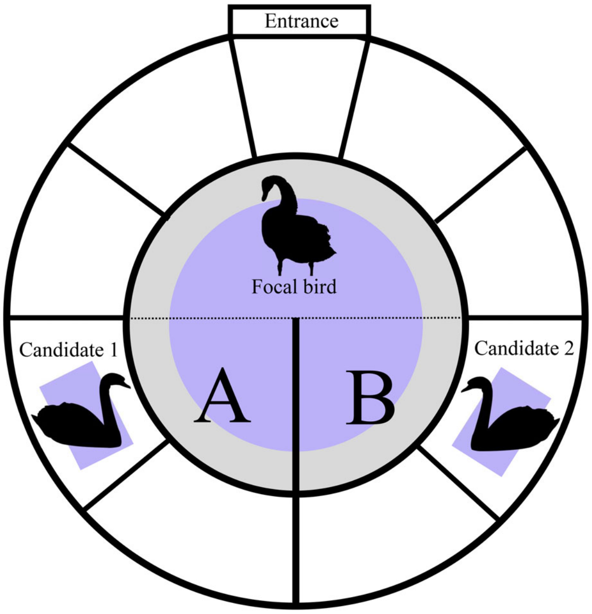

Figure 1. Overhead schematic of the arena used for swan association trials. The enclosure comprised a central moat (blue) bordered by a concrete walkway (grey) and surrounded by an entrance chamber (top) and eight enclosures of equal size. Two of the enclosures were occupied by candidate birds with which the focal bird could choose to associate. A visual barrier erected between quadrant A (nearest to candidate 1) and quadrant B (nearest to candidate 2) prevented the two candidate birds from seeing each other. During the barrier phase, we measured focal preferences by comparing the proportion of the trial spent in quadrant A versus quadrant B. At the beginning of the open phase, the enclosure doors were opened to allow all three birds to intermingle; during this period, we measured focal preferences by comparing the distance between the focal bird and each candidate.

pond bordered by a concrete walkway) surrounded by eight symmetrical chambers (each 5.0 × 3.0 × 2.8 m and containing a smaller rectangular pond of about 0.5 m^2). Two of the eight peripheral chambers contained a candidate bird, with the others left empty. These two peripheral chambers were visually segregated from each other using a wooden board and black builder's plastic, preventing candidate birds from seeing each other and so minimizing interactions between them.

In preparation for each association trial, two candidate individuals were introduced into their peripheral chambers and allowed 30 min to acclimate. Candidate birds within a trial were matched for body mass and head–bill size (both $P > 0.05$), but mismatched for their number of curled wing feathers (females: 'high' feather candidates 25.4 ± 0.35 se curled feathers, low 19.4 ± 0.41 se; males: high 25.7 ± 0.36 se, low 19.4 ± 0.39 se; all $P < 0.0001$). The mean difference between candidate birds (around six curled feathers) was similar to the difference found between paired and unpaired individuals in the wild (Kraaijeveld *et al.* 2004). To begin each association trial, we introduced the focal bird into the central chamber of the enclosure through a race at one end, giving it equal exposure to both candidate birds. From its point of release, the focal bird entered the water and could then swim towards either of the candidate birds. For the initial 30 min of the association trial, the focal bird could see the two candidate birds but was physically separated from them (the barrier phase). During this period, we recorded the proportion of the trial spent by the focal bird in the quadrant nearest each of the candidate individuals (Fig. 1). An experimenter then entered the enclosure and opened the doors to the peripheral chambers, allowing the candidate birds to leave the peripheral chambers or the focal bird to enter them (the open phase). We monitored the birds' movements for a further 30 min, estimating the distance (in metres) between the focal bird and each candidate bird at 1-min intervals. During this period, we also noted any overt instances of agonistic behaviour (e.g. pecking) between the focal and candidate birds. Because agonistic interactions were relatively rare (only observed in eight trials), we did not statistically analyse these data and report them only qualitatively. The birds were then recaptured and returned to their holding enclosures.

Six cameras were mounted around the upper walls of the central and peripheral chambers, affording a 360° view of the arena. Trial videos were saved to a digital video recorder (8-ch model, MPEG-4 DVR), allowing us to review the footage and score the birds' behaviour. Trials were scored by a single experimenter (A.C.K.) who was blind to each bird's degree of ornamentation.

We conducted 20 sexual trials and 20 social trials for each sex (80 trials total). Each individual participated in six trials, as: (1) the focal bird in one sexual trial, (2) the focal bird in one social trial, (3) a candidate bird in two sexual trials and (4) a candidate bird in two social trials. To give birds sufficient recovery time, we allowed an interval of at least 1 day between each of their trials. To control for any spatial biases, we alternated which chamber contained the more-ornamented candidate bird. For the sexual trials, we ensured that focal individuals had never interacted with either candidate bird in a previous trial; we did not maintain this requirement for the social trials, as birds were already familiar with each other from the same-sex holding enclosures. As a result of timing errors by the experimenters, some trial phases inadvertently ran shorter than the intended 1800 s (generally within the range 1700–1800 s, but as short as 1290 s in one extreme example). We nevertheless retained these trials in our dataset because focal birds had equal time to choose between each candidate bird regardless of trial duration. Due to a technical malfunction, data from one association trial (a sexual trial with a female focal) were lost.

Statistical analyses

For each combination of trial type (sexual, social) and focal sex (male, female), we used linear mixed models (LMMs) to test whether focal birds preferred one candidate bird over another based on feather ornamentation. We performed LMMs with the *lmer* function in the package 'lme4' (Bates *et al.* 2015), using R v. 4.1.2 (R Core Team 2021).

During the barrier phase, we assessed whether focal birds differed in their proportion of the total trial duration spent in the quadrant nearest to the low- or high-ornamented candidates. We tested this using four LMMs with proportion of the trial as the response variable, candidate bird ornamentation (number of curled feathers: high, low) and focal bird ornamentation (number of curled feathers: high, low) as fixed effects, and trial ID as a random effect. To test whether focal birds' own ornamentation influenced their preferences, we also initially included an interaction term between the two fixed effects, but this was non-significant ($P > 0.05$) in all analyses and was subsequently removed from the models.

During the open phase, we assessed whether focal birds differed in how closely they associated with candidate birds with low or high ornamentation. We tested this using four LMMs with mean distance between the focal and candidate bird (in metres) as the response variable. We included candidate bird ornamentation (high, low) and focal bird ornamentation (high, low) as fixed effects, and trial ID as a random effect. As above, we initially included an interaction term between the two fixed effects, but this was non-significant ($P > 0.05$) in all analyses and subsequently removed from the models. In the social trials only, the response variable was square-root-transformed before analysis to normalize the model residuals.

RESULTS

During the barrier phase, focal birds spent 76.54% ± 0.03% se of the trial in the two quadrants closest to the candidate birds, suggesting that their use of the central chamber was non-random and that they strongly preferred to associate with conspecifics. During this period, focal males spent similar proportions of the trial with each candidate bird, showing no preference for 'high' versus 'low' ornamentation in both sexual trials ($t = -1.37$, $P = 0.178$) and social trials ($t = -1.05$, $P = 0.302$) (Table 1, Fig. 3). Likewise, focal females spent similar proportions of the trial with 'high' and 'low' ornamented candidate birds (sexual trials: $t = -0.89$, $P = 0.377$, social trials: $t = 1.59$, $P = 0.121$) (Table 1, Fig. 2). The focal birds' own curled feather count did not influence their preferences as either an interaction or a standalone term in the model (Table S1).

During the open phase of the association trials, focal males showed a significant preference for candidate birds with more curled feathers, staying nearer to the 'high' ornamented bird than to the 'low' ornamented bird. This was the case during both sexual trials ($t = 2.19$, $P = 0.035$) and social trials ($t = 2.10$, $P = 0.043$) (Table 1, Fig. 3). Conversely, focal females showed no preference for candidate birds based on their number of curled wing feathers (sexual trials: $t = 0.19$, $P = 0.852$, social trials: $t = -1.16$, $P = 0.255$) (Table 1, Fig. 3). The focal birds' own curled feather count did not influence their preferences as either an interaction or a standalone term in the model (Table S1). During this phase, overtly agonistic interactions between the focal and candidate birds were relatively rare, observed in only eight trials

Table 1. Summary of swan behaviour (mean ± se) during two phases of an association trial, in which male or female focal birds could choose between two opposite-sex (sexual trial) or same-sex (social trial) candidate birds with different numbers of curled wing feathers.

	Male focal		Female focal	
Trial type	'High' candidate	'Low' candidate	'High' candidate	'Low' candidate
(a) Barrier phase				
Sexual trial	0.43 ± 0.07	0.30 ± 0.06	0.44 ± 0.08	0.34 ± 0.08
Social trial	0.45 ± 0.08	0.33 ± 0.07	0.28 ± 0.08	0.48 ± 0.10
(b) Open phase				
Sexual trial	3.24 ± 0.39	4.48 ± 0.41	3.42 ± 0.34	3.52 ± 0.39
Social trial	2.50 ± 0.33	3.70 ± 0.47	3.88 ± 0.40	3.25 ± 0.44

(a) During the barrier phase, the response variable was the proportion of the trial spent in the quadrant nearest to the 'high' or 'low' ornamented candidate. (b) During the open phase, the response variable was the mean distance (in metres) between the focal bird and the 'high' or 'low' ornamented candidate.

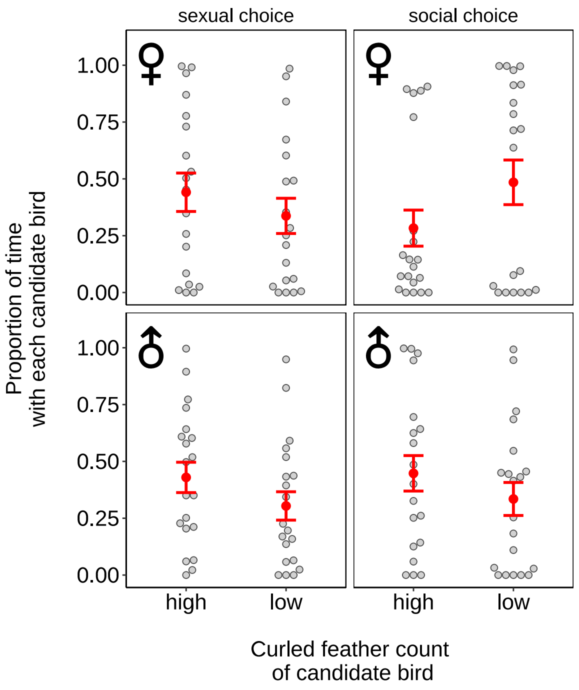

Figure 2. Focal preference for different levels of conspecific ornamentation during the barrier phase of the association trial. Focal females (♀) or males (♂) were allowed to choose between two candidate birds that differed in their relative level of wing feather ornamentation ('high' = more curled wing feathers, 'low' = fewer curled wing feathers). We conducted both sexual association trials (candidate birds were opposite sex to the focal bird) and social association trials (candidate birds were same sex as the focal bird). Plots show the proportion of the trial that the focal bird spent in the quadrant nearest each of the candidate birds (mean ± se, with raw data overlaid).

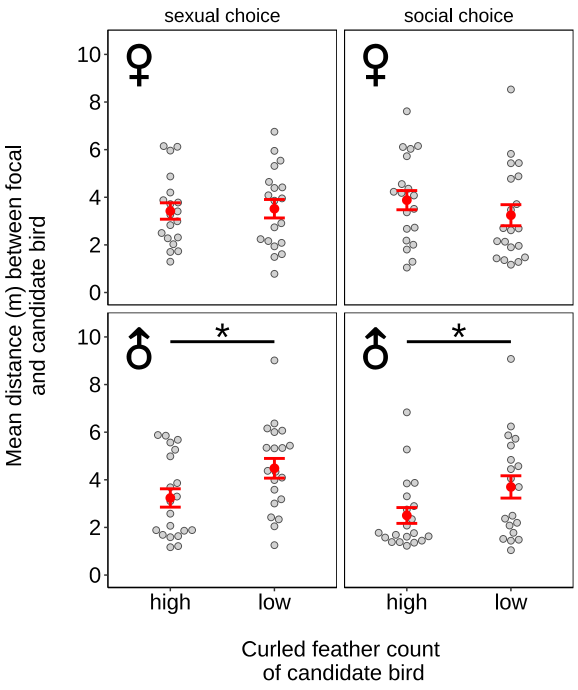

Figure 3. Focal preference for different levels of conspecific ornamentation during the open phase of the association trial. Focal females (♀) or males (♂) were allowed to freely associate with two candidate swans that differed in their relative level of wing feather ornamentation ('high' = more curled wing feathers, 'low' = fewer curled wing feathers). We conducted both sexual trials (candidate birds were opposite sex to the focal) and social trials (candidate birds were same sex as the focal). Plots show the mean distance (in metres) between the focal bird and each candidate bird (mean ± se, with raw data overlaid). Asterisks (*) indicate that focal birds associated significantly more closely (LMM: $P < 0.05$) with 'high' versus 'low' ornamented birds in that set of association trials.

(one female social trial, two male sexual trials and five male social trials).

DISCUSSION

Beginning with Darwin (1871), studies on the evolution of ornamentation have traditionally focused on sexual selection. However, this approach overlooks the many instances in which ornamentation is used to signal condition or dominance in non-sexual contexts (reviewed by Lyon & Montgomerie 2012). In this study, we provide evidence that a monomorphic plumage ornament in Black Swans (number of curled wing feathers) informs conspecific preferences in both sexual and non-sexual contexts. During the open phase of our association trials, in which the focal bird could freely mix with two conspecific candidates, focal males stayed nearer to the candidate that had more curled wing feathers. This was the case during both sexual trials (candidates were opposite sex to the focal bird) and social trials (candidates were same sex as the focal bird). In contrast, females did not express any preference for same- or opposite-sex candidate birds based on their wing feather ornamentation. These results highlight the importance of considering both sexual and social influences on the evolution of sexually monomorphic ornaments.

During our sexual association trials, focal males associated more closely with females that had a higher number of curled wing feathers. This supports our hypothesis that curled feathers—or some other closely associated trait—are serving an ornamental function in this species and may communicate an individual's quality as a prospective mate. Surprisingly, this preference was only expressed by focal males and not by females. Ornamentation research has traditionally focused on female mate choice but our results add to growing evidence that females can also be subject to sexual selection (reviewed by Hare & Simmons 2019), although we note that our trials only measured association preferences and not mate choice *per se*. Furthermore, focal males preferred the more ornamented female regardless of their own ornament elaboration, consistent with directional rather than assortative mate choice with respect to this trait. This suggests that the assortative mating previously observed in Black Swans (see Kraaijeveld *et al.* 2004) probably results from a mating market, whereby males compete for the most ornamented females and competition ultimately leads males to settle for partners whose ornamentation resembles their own (Baldauf *et al.* 2009).

We found similar preferences during the social choice trials: during the open phase, focal males preferred to associate with the more ornamented same-sex candidate whereas females showed no such preference. This suggests that curled feathers serve not only a sexual function but also an additional social function between male conspecifics (Kraaijeveld *et al.* 2007a). Researchers studying the evolution of ornaments often emphasize the role of sexual selection while neglecting the potential role of social selection (Kraaijeveld *et al.* 2007a, Tobias *et al.* 2012). When individuals compete for non-sexual resources, such as food, territories or nesting sites, selection is predicted to favour ornamental traits that positively influence the outcome of social interactions by signalling the superior quality of the bearer (Wolf *et al.* 1999, Kraaijeveld *et al.* 2007a). Although the social functions of ornaments have received less research attention than sexual functions, several examples have been reported in birds. Ornamental plumage colour reflects social dominance in Common Waxbills *Estrilda astrild* (Cardoso *et al.* 2014, Beltrão *et al.* 2021) and in female Indian peafowl *Pavo cristatus* (Earl *et al.* 2022). In American Goldfinches *Spinus tristis*, bill colour—a monomorphic trait—signals social status in females but not males (Murphy *et al.* 2009, 2014). In Black Swans, too, the number of curled wing feathers may indicate social dominance, as highly ornamented individuals are more likely to win agonistic same-sex interactions (Kraaijeveld *et al.* 2004). Male swans experience more intense social competition over resources compared with females (e.g. they are involved in more agonistic interactions; Kraaijeveld *et al.* 2004), which may explain why focal males in our experiment used wing ornamentation as a social signal but females did not. However, the swans' behaviour in these social trials was potentially confounded by pre-existing dominance hierarchies. In contrast to the sexual trials, the animals in each social trial were familiar with each other, having been in many cases sourced from the same site and held together in a communal holding enclosure for the duration of the study.

It is unclear why males showed no preference for more ornamented birds during the barrier phase of our trials. It is possible that the mesh barrier limited the focal birds' ability to visually assess each candidate or that candidate birds inside the pens were less likely to exhibit behaviours, such as threat displays, that showed off their curled wing feathers. Because males' preference for high ornamentation was only present during the open phase of our association trials—when the three swans could intermingle—we cannot exclude that this result was partly the result of the behaviour of the candidate bird. This could be the case if, for instance, an individual's ornamentation is linked with personality traits such as activity, sociability or aggressiveness (e.g. Thys *et al.* 2020, Fülöp *et al.* 2021). Future studies should experimentally manipulate the number of curled wing feathers to disentangle this particular trait from any others that could potentially drive these patterns.

Two main hypotheses have been proposed to explain the evolution of mutual ornamentation: (1) monomorphic traits are expressed in both sexes but are non-functional in females, occurring only due to genetic correlation between males and females (genetic correlation hypothesis) and (2) monomorphic traits occur due to similar selection pressures acting on both sexes (mutual selection hypothesis) (Kraaijeveld *et al.* 2007a, Nolazco *et al.* 2022). Previous work on Black Swans arguably favoured the genetic correlation hypothesis, as the number of curled feathers reliably predicted body condition only in males (Kraaijeveld *et al.* 2004). However, our experimental results suggest that the male preference for highly ornamented conspecifics in both sexual and social contexts could drive the development of this ornament in both sexes. Importantly, although sexual and social selection are often studied as separate processes, they are not mutually exclusive: a single ornamental trait may simultaneously function both in mate choice and in competition over sexual and non-sexual resources (Kraaijeveld *et al.* 2007a, Tobias *et al.* 2012). For example, the ultraviolet crest coloration of Blue Tits *Cyanistes caeruleus* is known to both influence male mate choice (Hunt *et al.* 1999) and mediate male–male social interactions (Rémy *et al.* 2010).

Our results suggest that the curled wing feathers of Black Swans, which are present in both sexes, are used by males as both a sexual and social signal. This supports the hypothesis that sexually monomorphic ornamentation can result from a combination of sexual and social selection (Kraaijeveld *et al.* 2007a) and may help to explain the evolution of monomorphic ornaments in systems where only one sex shows a sexual preference for that trait. Our results serve as a reminder that studies that focus exclusively on sexual preferences risk mischaracterizing what may be more generalized preferences for ornamentation.

We wish to thank Sarah Thompson for her major contributions to this study, including conducting the mate choice assays, and Patrick-Jean Guay for his involvement in the project. We are grateful to Mick Smith and other Parks Victoria staff for permission to conduct the work at Serendip Sanctuary and for their assistance with many logistical issues, ranging from the provision of bore water to food provisioning. We thank associate editor Lei Cao, editor Rebecca Kimball and one anonymous reviewer for comments that improved the manuscript. Funding was provided by an Australian Research Council Discovery grant (DP0558607, to R.A.M. and M.A.E.). The procedures used for this study were approved by the Animal Ethics and Experimentation Committee of the Faculty of Science, University of Melbourne (register no. 0705887.4) and performed under permit from the Victorian Department of Sustainability and Environment (10004585).

AUTHOR CONTRIBUTIONS

Andrew C. Katsis: Investigation; formal analysis; visualization; writing – original draft; writing – review and editing. **Mark A. Elgar:** Conceptualization; methodology; funding acquisition; writing – review and editing; resources; supervision. **Raoul A. Mulder:** Supervision; resources; conceptualization; methodology; writing – original draft; writing – review and editing; investigation; funding acquisition.

CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

ETHICAL NOTE

None.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available in the Supplementary material of this article.

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Received 15 May 2025;
Revision 18 July 2025;
revision accepted 28 July 2025.
Associate Editor: Lei Cao

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Output from LMMs measuring focal bird preferences during the barrier phase of the association trials.

Table S2. Output from LMMs measuring focal bird preferences during the open phase of the association trials.

Data S1. Excel file containing all data used for analysis.

Data S2. R code used for all analyses.